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Adaptive Control Responses to Behavioral Perturbation Based Upon the Insect

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14. ABSTRACT

The Munitions Directorate at Eglin AFB FL supported research at Case Western Reserve University (CWRU) in Cleveland OH describing transitional behaviors in insect walking and in flight. Quantitative descriptions of the complex decisions that a cockroach makes in deciding to climb over or tunnel under a barrier allowed the examinations of discrete brain lesions in order to pin point where and how these decisions are made. Documentation of turning movements developed hypotheses regarding how descending cues might alter local reflexes to turn the animal while retaining stability. Lesions in the brain and subsequent recordings demonstrated how the descending commands might be formulated within the brain. A robotic leg was developed (hardware model of the system) and could play a critical role in testing our hypotheses at a systems level. The obtained results also positioned CWRU to move ahead with new funding initiatives. The brain recording and stimulation projects that were initiated during this research effort are now funded by an NSF grant to the Ritzmann laboratory at CWRU. In addition, the projects that were undertaken to understand the alterations that occur at the local control level in response to descending commands is being pursued as a proposal to AFOSR.

15. SUBJECT TERMS

Descending neuron-control, orientation, kinematics, biorobotics, cockroach

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EXECUTIVE SUMMARY

One of the distinguishing features of animal behavior is the capacity to respond quickly and efficiently to a range of perturbations affecting the animal's ambulatory progress. Rather than switching to new control algorithms, animals adapt to these changing conditions without hesitation by modifying activity in existing neural circuitry. If this capacity to alter control in response to ever changing conditions could be captured in the control architecture of artificial devices ranging from robots to missiles, it would greatly increase their ability to perform missions independently under real world conditions. However, we are only beginning to understand how animals solve these problems. Insects, which are the most successful animals in the world and certainly among the most agile, provide several important technical advantages for studying neural control of adaptive behavior. It is therefore believed that a comprehensive study of insect neural control schemes can greatly benefit designs for man-made vehicles.

During this technical effort, scientists from Case Western Reserve University (CWRU) investigated how insects identify and characterize obstacles and then use that information to command alterations in forward locomotion all in a matter of milliseconds. A range of insect preparations already provide considerable neurobiological information on the processing of sensory information within brain regions and the corrective actions that occur in local motor circuits found in the thoracic ganglia. However, very little is known about the linkage between these two regions and it is here that they focused there attention. Although they chose to focus upon walking insects, because of technical advantages to these preparations, they contended that the control rules that were uncovered could be generalized to any animal or vehicle that must move through three dimensions and respond quickly and efficiently to barriers in its path. This assumption was tested by comparing data from cockroaches that move primarily by legged locomotion with similar data from moths that move primarily by flight. Further, they incorporated the resulting control rules into both software simulations and robotic systems.

INTRODUCTION

Novel developments of technical devices to solve our most serious problems can benefit from an intelligent interplay between biology and engineering. Some of the most challenging problems to technical development have already been solved by animals through millions of years of evolution. Very few vehicles can match the agility of legged animals as they move through complex natural terrains. Nevertheless, merely copying animal systems will not provide optimal solutions. After all, manmade devices often surpass specific capabilities of any animal system. For example, man has managed to develop devices that are more powerful, faster and can fly higher than any animal could every hope to achieve. Moreover, issues of scaling and materials, make direct mimicry a less than optimal strategy. Rather, what is required is an intelligent strategy for lifting rules from biological systems and incorporating them appropriately into control architecture for robotic devices.

The capabilities of animals have lead several groups to examine biological systems as inspiration for agile and efficient man-made vehicles. The strategies that have been employed in these studies vary greatly (Ritzmann, Quinn, Watson and Zill, 2000). On one hand, biologists may make detailed observation of relevant aspects of movement and provide these data to engineers who implement them as much as is possible in their devices in order to capture the animal's dexterity. At the other extreme, the engineers design a device using standard engineering practices and then turn to biological systems as a resource for solutions to specific problems. In either of these cases, the specific goal is the development of improved devices.

The reverse relationship has also been fruitful. Robotic devices have been developed by several biological groups specifically to test neural control and mechanical hypotheses. Webb (2001) utilized wheeled robots to test notions about cricket song recognition as did Grasso in testing hypotheses regarding olfactory guidance in lobsters (Grasso, Dale, Consi, Mountain and Atema, 1996). Srinivasen implemented his notions about visual navigation in bees on robotic devices to test their real world capabilities (Srinivasan and Zhang, 2000; Srinivasan, Zhang and Chahl, 2001). Dickinson built a robotic device to measure forces associated with flight behavior in insects (Dickinson, Lehmann and Sane, 1999).

CWRU proposed to span both of these goals, by building upon the unique biology-engineering relationship that has developed over 15 years at Case Western Reserve University. The insect locomotion studies that were proposed initially emphasized biological questions. However, the resulting control rules were implemented in existing robotic devices via dynamic simulation tools that are currently available to our group. This effort will not only result in more capable devises, but also provided hardware models for generation of new hypotheses that can be tested by further biological experimentation. In this way, the biological data will lead to engineering advances that will lead back to greater understanding of the original biological systems.

SCIENTIFIC APPROACH

Natural environments are heterogeneous and dangerous places. Although some natural conditions can be tamed by removing trees and building flat roads, we cannot remove all barriers. Consequently, locomotion through natural terrain requires rapid decision making and quick alterations in movement trajectory. Most animals handle these problems very efficiently. In particular, insects can run or fly

smoothly through environments that are strewn with objects that often require them to rapidly react to barriers in order to reach their ultimate goals.

A considerable amount of effort in motor control has rightly focused upon the basic steady-state movements that animals use to move across a flat surface. Unfortunately, relatively little attention has been paid to the *transitional behaviors* that allow animals to efficiently negotiate natural environments, in spite of the fact that it is an understanding of these very responses to perturbation that would have the greatest impact upon the development of man-made devices. Rapid adjustments approaching animal-like responses would clearly benefit the design of autonomous vehicles. Currently, most of these problems are handled by a driver, pilot or tele-operator. It is not only inefficient to rely on a person to make all these adjustments, but in many conditions the delays may be so long that a rapidly moving vehicle would crash or fail its mission before the adjustment is made. Devices that are moving through dangerous regions may move slower, but this advantage is lost by even greater delays in communication between the device and a driver positioned at a safe distance from the operation. Consider a robotic vehicle searching for survivors in a collapsed building. If the robot encounters a barrier to its movement, but must rely on a signal to a tele-operator outside the building, it may crash or become irreversibly stuck before a sensor reports the problem to the operator, he or she makes a decision and the correction signal reaches the robot. Similar issues are faced by both missiles and their targets as they enter the endgame strategies of pursuit (Cloutier, Evers and Feeley, 1989). By empowering control systems with animal-like responses, reaction time would be greatly reduced and problems posed by barriers and other perturbations could be easily avoided.

In the past, CWRU has focused upon transitional behaviors in walking insects, because a considerable amount of information is already available for these systems and the necessary biological experiments can be readily performed on cockroaches. These advantages make walking insects particularly attractive for the kinds of studies that we are proposing. Nevertheless, it should be possible to generalize the control rules that result from these studies to any animal or vehicle that moves through three dimensions and encounters obstacles in its path. To do this, one must identify the components of the animal or vehicle that generate thrust, turning (yaw) and pitch as well as appropriate sensors for detecting and characterizing the barriers. One must then characterize the link between detection and actuation.

To test this notion, CWRU compared the results from their walking studies to control in flying insects. This was done in two ways. First, control of wing movements in *Blaberus discoidalis*, the same insect that is being studying for walking, was examined. *Blaberus* will readily generate wing movements in response to wind directed at its head. Therefore, the role of individual interneurons during walking and flying within the same animal could be examined. However, *Blaberus* does not fly freely very well. Therefore, the results on data taken on the hawkmoth, *Manduca sexta*, which is a very strong flyer and is comparable in size to *Blaberus discoidalis*, was also compared. A thorough examination of descending control for both walking and flying behaviors was beyond the scope of a three year project and CWRU was much further along in walking than in flying. Therefore, CWRU concentrated their efforts on transitional behaviors involved in walking, while examining flying in sufficient detail to test the notion of generalization.

The control regions for insect locomotion can be broken up into three regions (Fig. 1). The sensors located on the head detect barriers to forward locomotion and project to brain regions were they are processed and integrated with information from other sensors and data on motor activities. Based upon

this information, commands are formed in the brain and sent via the cervical connectives to local motor control regions in the thoracic ganglia. The head sensors (antennae and visual systems) are comparable in the cockroach and the hawkmoth (Fig. 1). The motor commands descend through a limited number of cervical interneurons to local motor control systems in thoracic ganglia. Here differences will occur. In the cockroach the local systems will control six unique pairs of legs that alter movements to generate variations in turning (yaw), body attitude (pitch), and forward speed (thrust). In the moth, alterations in wing movement will generate similar motor effects as the animal flies. Similarly wing control in the cockroach will employ different sets of motor neurons and muscles than those that control the legs.

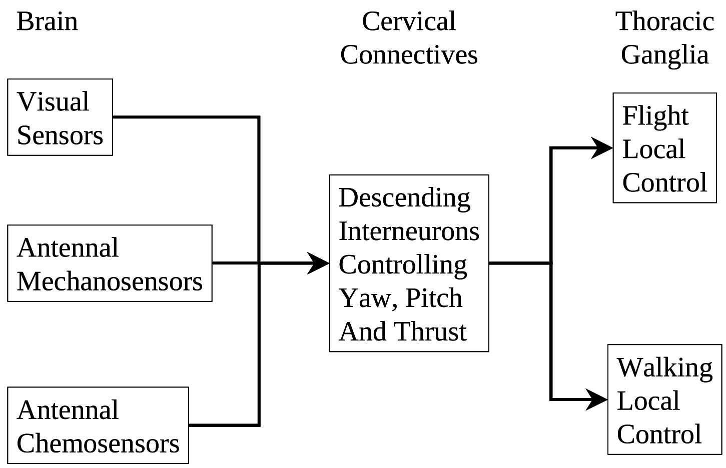

Figure 1. Hypothetical arrangement of control elements for transitional behaviors involved in flight and walking.

Clearly, a total understanding of the issues presented by either walking or flight control is beyond the scope of any short term investigation. Fortunately, many other investigators are currently working on several aspects of the problem. New information is becoming available on sensory processing in insect brains (Gupta, 1987) and reflex responses in motor circuits (Bässler, 1998; Burrows, 1996). What is almost totally lacking is an understanding of the linkage between these two regions. Specifically, the question that was pursued was: How do behavioral decisions that are arrived at in the brain alter specific motor activity?

CWRU proposed a comprehensive set of biological experiments on both walking and flying insects that made tremendous strides in establishing how this linkage occurs. The resulting principles were then modeled in dynamic simulation and implemented in robotic systems that were currently available to the research team. These latter aspects of the proposed work, allowed the test and refinement of the hypotheses in real world systems, and assured that the resulting system-level control principles could be incorporated into a range of man-made devices that have importance to Department of Defense missions.

The specific aims of this project were to:

1. Identify and characterize sensors on the cockroach head that are associated with detection and evaluation of objects that are barriers to forward locomotion and compare the actions of these structures to analogous sensors on the moth. The roles of antennae, ocelli and compound eyes in obstacle detection and evaluation under various conditions such as light level and walking speed were

examined. Differences in their functions under walking and flying behaviors were also examined.

2. Identify descending interneurons that conduct information and decisions from brain regions that process information from sensors on the head to motor centers in thoracic ganglia that control leg movements and compare to descending interneurons used in flight. The observation that in many insects relatively few descending interneurons exist (Staudacher, 1998), suggests that the same cells may be used for multiple behaviors such as walking and flying.

3. Using a tethered preparation, characterize the motor changes that occur in order to transition from walking to turning and formulate hypotheses regarding how descending activity brings these changes about. The hypothesis suggests that this is where walking and flying control diverges. By comparing the motor changes found in walking to those in flying, it could be determined whether similar descending cues can access both systems and if so, whether control principles generalize according to movement axes such as yaw, thrust and pitch.

4. Implement control strategies in a range of legged robotic systems. By implementing the rules that are developed in this study into control systems for existing robotic devices, the hypotheses under real physical conditions could be tested, establish their capacity for use in robotic vehicles, and develop new hypotheses for further biological tests.

BACKGROUND INFORMATION: INSECT ANATOMY

Arrangement of Insect Thoracic Nervous Systems

A complex mix of sensory inputs and endogenous pattern generation circuits control movement in virtually all legged animals. The neural control systems are divided into specific locations within the animal's central nervous system. An insect has six legs with each pair located on a separate thoracic segment (Fig. 2) (Burrows, 1996). Flying insects possess one to two pairs of wings located on the second and (where two pairs are present) third thoracic segments. Within each segment the nerve cord expands to form a ganglion that contains approximately 1000 interneurons and motor neurons that control movements associated with that segment.

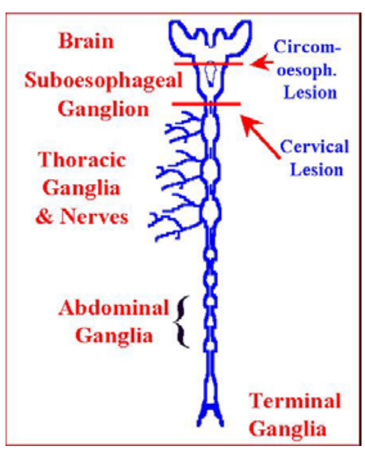

Figure 2. Diagram of cockroach nervous system showing Brain, Suboesophageal ganglion, Thoracic ganglia and abdominal ganglia.

Each pair of legs is controlled by a separate thoracic ganglion. Location of two lesions are also noted for discussion in the following. A considerable amount of behavioral and neurobiological data have

been amassed regarding the neural circuits found in the thoracic ganglia. These so-called local control circuits contain the motor neurons that directly control leg muscles as well as local interneurons that serve to group sensory information from the leg and coordinate actions of the various muscles within different leg segments (Burrows, 1989). These elements are influenced by pattern generation neurons that set the rhythm for oscillatory behaviors such as those that initiate leg movements during walking and running. There are also interganglionic interneurons that coordinate actions between each leg to generate such movements as the tripod gait (Cruse, 1990; Schmitz, Dean, Kindermann, Schumm and Cruse, 2001). Sensory receptors located on and within the leg play important roles in monitoring leg movement during walking (Zill, 1990).

A case can and has been made that much of the control of leg movements during walking, even over uneven terrain, can be attributed to the local control circuits in the thoracic ganglia (Cruse, 1990; Schmitz, et al., 2001). Indeed, the rules by which this control can be accomplished provide the basis for locomotion controllers of several hexapod robots (Beer, Chiel, Quinn and Ritzmann, 1998). However, observations dating back to the work of Roeder (1937) have clearly shown that insects do not walk in a normal tripod gait after lesioning the neck connectives (cervical lesion in Fig. 2), thereby isolating the thoracic ganglia from neural centers in the head, including the brain and suboesophageal ganglion. We have repeated these experiments on animals that were maintained alive by hand feeding for up to two months post lesion (Ridgel, Alexander, Mu, Ritzmann and Strausfeld, 2002). We found that over the course of 10 days, stepping did increase, and some coordination returned between left and right legs of individual thoracic segments. However, intersegmental coordination never returned and joint movements were much reduced. Injection of the neuromodulator octopamine increases the number of steps taken, but does not improve intersegmental coordination. Rarely, step cycles corresponding to the "classic" alternating tripod gait *are* produced. Thus, it appears that the thoracic circuitry that organizes action into a tripod gait does exist in the thoracic ganglia. However, that coordination is not readily expressed without connection to the higher centers.

Roeder (1937) also reported that a lesion anterior to the suboesophageal ganglion (circumoesophageal lesion in Fig. 2), which sits in the head between the brain and the thoracic ganglia, results in an animal that walks constantly. We also confirmed and extended this observation. Blaberid cockroaches with bilateral lesions of the circumoesophageal connectives walk interminably in a perfect tripod gait. These animals can move around, over and under barriers. However, since they lack input from the sensory processing regions of the brain, they do not do so like an intact animal. Intact animals detect barriers through actions of sensors such as eyes and antennae. Posture is then altered well before reaching the barrier. As a result, they seamlessly move over, under or around the block without bumping into the obstacle. Animals with circumoesophageal connective lesions (CoCL) do not show this coordinated behavior when challenged with an obstruction. Rather, they alter their movements only *after* running into the barrier. For example, they will climb up a block by simply pushing forward until the body bends upward and slides up the front surface.

In addition to the obvious sensory deficits described above, CoCL animals also have some surprising motor problems. They have difficulty walking up inclines, probably because they do not adjust walking speed to new conditions. They also have difficulty flexing thoracic segments causing them to high-center badly when climbing over blocks.

From these observations, it can be concluded that neural circuits within the suboesophageal ganglion promote forward locomotion and the expression of appropriately coordinated leg movements.

Furthermore, the normal transition from forward movement to turning or climbing behaviors in anticipation of a barrier requires input from even higher centers found in the brain. Thus, a critical aspect in the control of transitional behaviors relies upon the neural interactions among brain, suboesophageal ganglion and local control circuits in the thoracic ganglia.

Block Climbing: An Example of Transitional Behavior

CWRU recently described the kinematics and motor activity associated with one transitional behavior (Watson, Ritzmann and Pollack, 2002; Watson, Ritzmann, Zill and Pollack, 2002). As a cockroach approaches an 11 mm block, it rears upward by rotating the middle legs and pushing downward (pitch). It can then place its front legs on top of the block and push its body up and over the obstacle by extending the powerful rear legs (thrust). It typically performs the critical rearing movement without making significant contact with the front legs along the leading edge of the object. Thus, it appears to detect and measure the block using sensors located on its head and then to direct the appropriate movements to efficiently get over the barrier.

Block climbing, thus, requires a direct interaction between sensors located on the head and sensory processing regions within the brain. The resulting motor commands descend through interneurons in the cervical connectives to thoracic ganglia where they must be interpreted by local neural circuits specific to each motor plant (legs or wings). The local circuits each rely upon proprioceptive reflexes to match the resulting movements to ongoing external and internal conditions. The properties outlined here make block climbing an excellent transitional behavior on which to focus for studies on motor control in complex terrain.

RESULTS

The “Adaptive Control Responses to Behavioral Perturbation” project was very successful in discovering new information on how insects control turning maneuvers. Great headway was made in both biological and engineering aspects of the project. Moreover, strong foundations were developed for future studies. The results will be described three segments. First, the progress in understanding local and descending control in cockroach transitional behaviors will be described. Then the progress in understanding similar aspects of moth flight, which was included in the proposal to test the universality of our hypotheses, will be described. Finally, the progress in robotic implementation that will ultimately provide a unique opportunity for both testing and implementation of our notions of control in complex behavior, will be covered.

Transitional Behaviors in Cockroach

The goal for this project was to understand how the insect’s nervous system generates transitional behaviors to deal with barriers to forward locomotion. Previous work clearly demonstrated that cockroaches get around objects in their path by evaluating the barrier with sensors on their head and using the information that they gain to alter leg movements (Watson et al., 2002a; Watson et al., 2002b). The decisions made in climbing and turning behaviors using high-speed video to document the insect’s decisions were further examined. These data were reported in two posters at the last two meetings of the Society for Neuroscience (Harley et al., 2005; Harley et al., 2006) and are currently being written up for publication in a journal article. Markov chain models demonstrated that the cockroach uses information gained by tapping the object with its antennae to guide climbing

movements over a block. If the block is replaced with a shelf, the cockroach is now faced with the choice of either climbing over or tunneling under the object. The choice taken is determined by whether the antennae touch the shelf from the top or form underneath. Tapping from the top generates climbing, while touching from underneath causes tunneling. Ambient light also seems to be important. In bright lights, the cockroach tends to tunnel twice as much as it climbs, while in low light the probability of either behavior occurring is equal.
More information about what is being gained from the antennae was documented by ablation experiments. Ablation of antennae alters the point at which the climbing commences. The shorter the antennae are, the closer the cockroach gets to a block before starting to rear up. Interestingly, if the antennae are completely removed, the cockroach completely alters its climbing strategy. Rather than using a controlled rearing behavior, it now uses elevator reflexes. In this latter strategy, the cockroach bumps its leg repeatedly onto the front surface of the barrier. Each contact causes the cockroach to lift its leg higher until it is placed on the top surface of the block. This strategy is also used by insects with circumoesophageal connectives lesioned to disconnect the brain from the thoracic ganglia.

Local Control in Cockroach Turning and Climbing

At the outset of the project, work was started on two distinct areas thought to be involved in the neural control systems underlying turning behavior; (1) direct local control systems within the thoracic ganglia and (2) descending commands formulated within specific brain regions. To investigate these issues in cockroaches, a tethered preparation that allows us to study turning movements in detail was developed. The insect is placed over a lightly oiled glass plate and forward movement is constrained by two pins placed in the pronotum (dorsal cuticular shield). In this condition, the cockroach walks normally but its body remains in one place. Under these conditions, very detailed kinematic and neurobiological observations even extending to intracellular recording were made. It was demonstrated that turning movements could be generated in the tethered preparation by pushing on one antenna. Essentially, the animal goes from a very symmetrical left-right set of joint movements during walking to a decidedly asymmetrical set of movements during turning. In the leg that would be on the outside of the turn, motor and joint activity is similar to walking, but directed more laterally. However, in the inside leg, the distal femur-tibia (FTi) joint increases extensor activity and joint velocity, while the more proximal coxa-trochanter (CTr) joint decreases depressor motor activity and shows very reduced joint movement (Fig. 3). Most importantly, these joint extension movements occur during swing phase in the inside leg, rather than during stance as in all other walking movements. A paper that describes these changes in detail was published in the *Journal of Comparative Physiology A* (Mu and Ritzmann, 2005). That paper proposes an hypothesis for how the changes are generated, suggesting that descending commands alter critical parameters in the local control reflexes within the thoracic ganglia then allow the sensori-motor reflexes to push the system to a new stable (turning) state.

Biological experiments were initiated to test this hypothesis and to developing a robotic device (described later) that will provide a unique opportunity to establish how realistic this explanation is under real physical conditions. In the biological experiments, it was asked whether movements that are similar to inside turning can be generated in animals when commands descending from higher brain centers are completely eliminated. This was completed by cutting the two circumoesophageal connectives that link the brain to the suboesophageal ganglion. These circumoesophageal connective lesioned (CoCL) animals walk continuously. Using dual high-speed video systems and three dimensional motion analysis software, very careful comparisons among walking, turning and searching movement both in intact and lesioned insects could be made. On the tether, searching movements by

the legs can be evoked by simply dropping the substrate away from the animal. At the leg, this action resembles the swing phase extension seen in inside turning. The FTi and CTr joint movements and associated motor activity are very similar to inside turning. Thus, the critical parameter for turning appears to be the swing phase extension implying that the primary target of descending commands would be muscles that lift the leg to begin swing. Additional experiments are currently being performed.

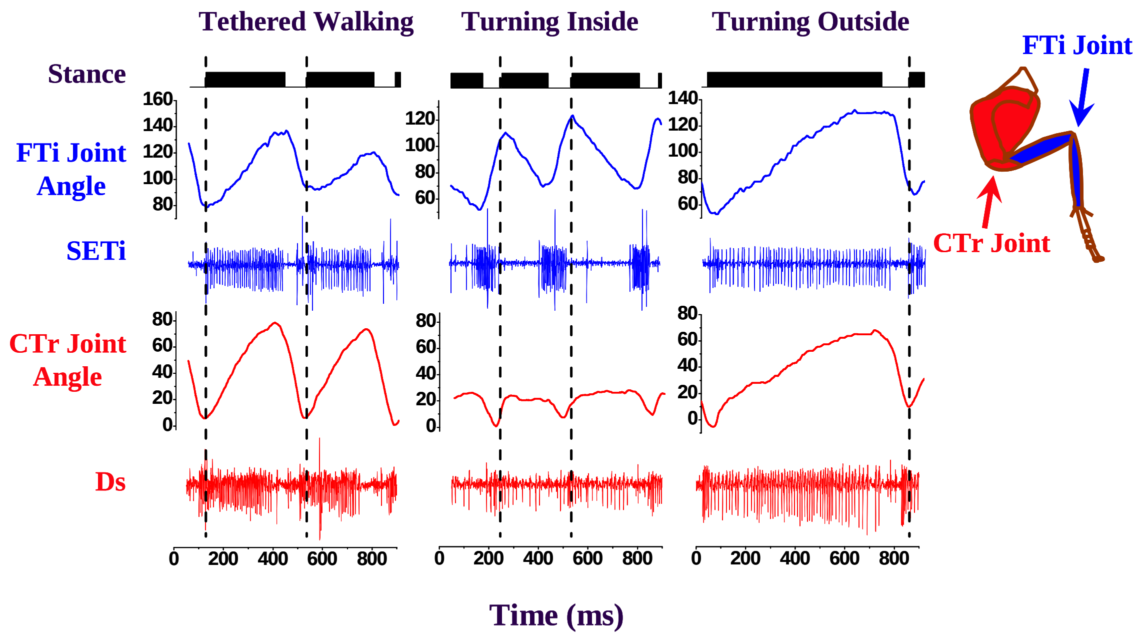

Figure 3. Motor activity and joint movement from tethered preparation showing walking (first column) and bilateral activity that occurs during turning (second and third column). Note the change that occurs in the motor activity and joint kinematics in the inside leg. Inset shows the two joints depicted here.

In addition to the three dimensional reconstruction of leg movements, students in the Quinn and Ritzmann CWRU laboratory teamed up to develop a computer simulation of middle leg movements that allowed us to examine the effects of each leg joint movement upon the actions of the foot. This model was presented at the recent meeting of the Society for Neuroscience and was very enlightening (Mu et al., 2006). Many of the effects of joint changes between walking and turning confirmed our previous hypotheses. However, some very subtle effects were also found to be very important. For example, in walking, the proximal CTr joint extension and Ds activity commences slightly before the more distal FTi joint extension and its SETi motor neuron.

In contrast, the inside leg of the turning animal has this timing reversed, with the FTi joint preceding the CTr joint. This subtle change is actually critical to the foot actions associated with joint extension, which occurs in stance during walking but in swing in inside leg turning actions. If the CTr joint extends first the foot drives into the substrate and FTi extension can then only contribute to downward force. However, if the FTi joint extends first, the foot is directed upward contributing to the swing phase extension associated with turning.

Finally, it was demonstrated that descending signals from the brain have profound influences upon

local control reflexes within the thoracic ganglia. It was demonstrated that movement of the femoral chordotonal organ that monitors joint position of the FTi joint evokes activity in both the motor neurons that control that joint and those that control the next proximal CTr joint. In the latter, Ds motor activity is enhanced when the chordotonal organ is extended and inhibited when it is relaxed. These inter-joint reflexes were previously described for stick insect (Hess and Büschges, 1999), but this is the first description in cockroach. In insects that had experienced bilateral lesion of the neck connectives or the circumoesophageal connectives, thereby removing descending activity, both the excitatory and inhibitory reflexes were greatly reduced or eliminated in the inter-joint but not the intra-joint reflexes (Fig. 4). This suggests that descending cues target interjoint reflexes as the animal alters coordination of joints to perform different behaviors.

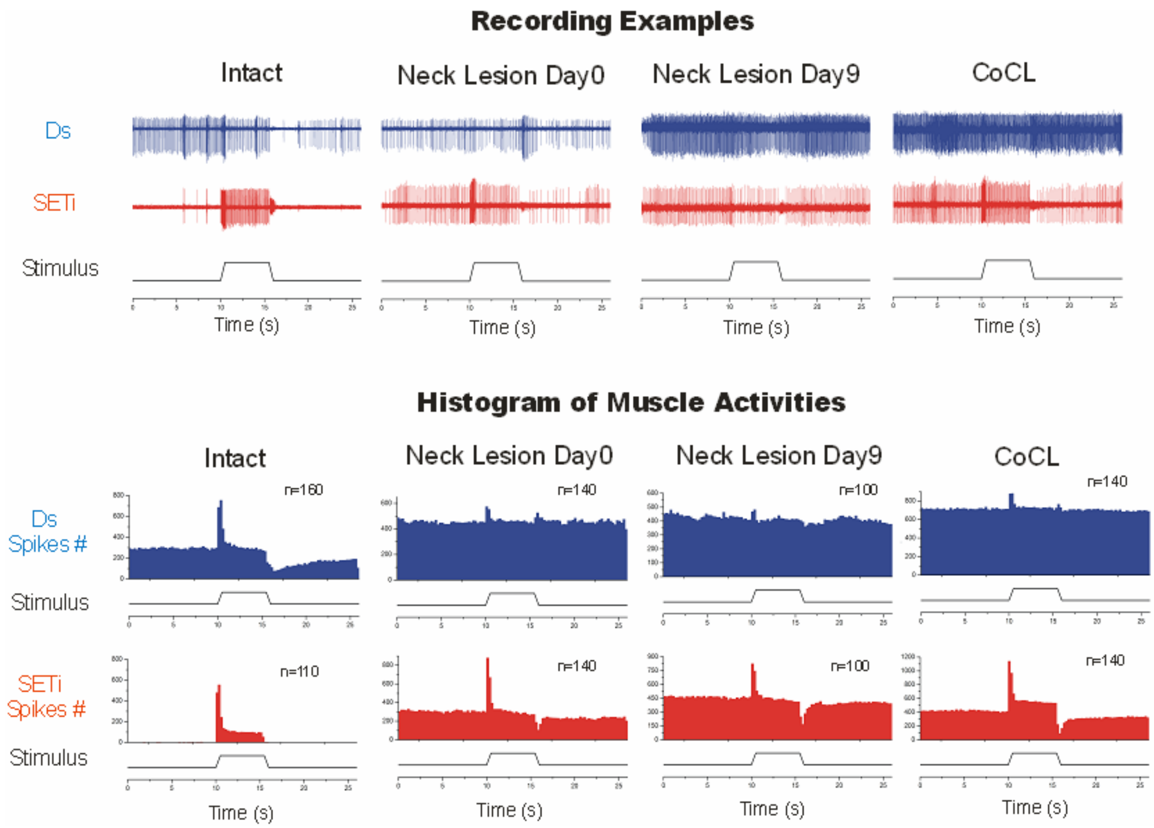

Figure 4. In intact insects, movement of the femoral chordotonal organ evokes reflex responses in both SETi (motor neuron controlling the home FTi joint) and Ds (motor neuron controlling the next proximal joint. However, lesion of neck connectives or circumoesophageal connectives (CoCL) disrupts the excitatory and inhibitory intersegmental reflexes to Ds.

Processing in the Brain

At the other end of the system, research was initiated to examine the descending commands that generate these changes. Under the Eglin grant, turning behaviors in insects with lesions to various regions of the brain were examined. These experiments clearly demonstrated that the neuropils that make up the central body complex (CBC) are critical to control of these transitional behaviors. Lesions that involve the CBC showed significantly higher incidence of abnormal turning behaviors such as turning the wrong direction or failure to turn at all after contacting an obstruction. In contrast,

sham operated animals or animals that had lesions distant from the CBC turned normally. These data were reported in a paper that was recently accepted to the *Journal of Comparative Physiology A* (Ridgel et al., 2006).

These data suggest descending commands that are formulated in the CBC provide descending influences that alter walking movements. To examine these commands, two new techniques: multi-unit recording in restrained cockroaches and stimulation in tethered insects were developed. Multi-unit recording is a new technique that can now be performed routinely in the brain. Sixteen-channel probes obtained from Michigan Probes were used. They were connected to a Neurolynx recording system, and then inserted into various brain regions to record brain activity from neurons at each recording site. Cluster cutting software was then used to identify individual units within the raw data. For example, in restrained animals, the antenna were moved back and forth several times with servo motors to identify units that respond to antennal movement in either direction or, more specifically, movement to the right or left side of the animal (Fig. 5).

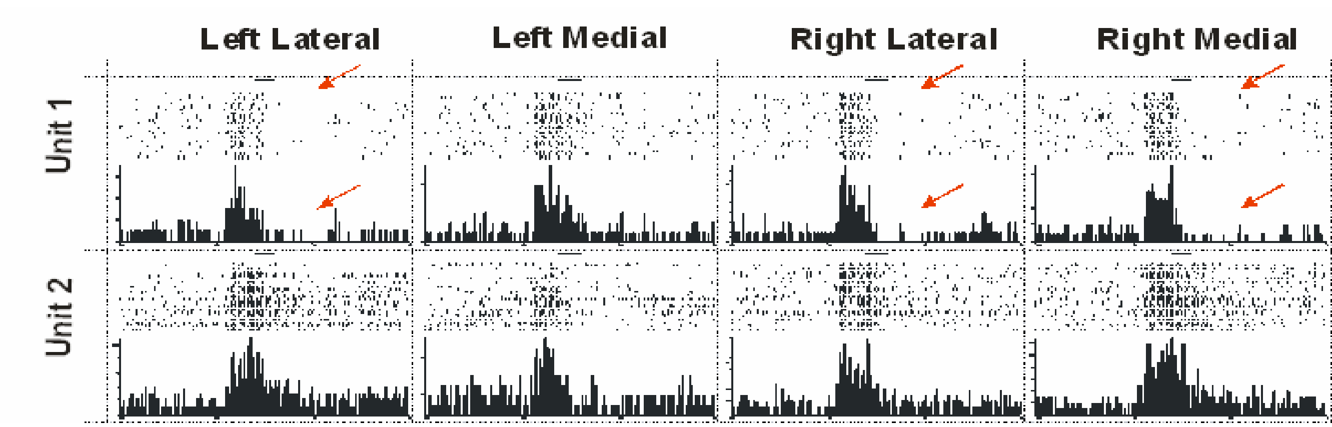

Figure 5. Raster displays and peri-event histograms of two brain units recorded in the central complex showing clear responses to movement of either antenna either medially or laterally. Unit 1 also showed inhibition following the positive response (red arrows).

In the stimulation paradigm, fine wire bundles are inserted into the brains of tethered animals. Regions like the CBC or its output regions (the lateral accessory lobe – LAL) were stimulated, and then the effects on movement were examined using high-speed video. Regions were found that could evoke turning in animals that are walking forward. In other brain regions, stimulation caused the insects to simply walk faster. Results from both of these paradigms were reported on at the recent meeting of the Society for Neuroscience (Pollack et al., 2006). They will serve as the basis for more detailed recording and stimulation experiments that will be conducted under an NSF grant to the Ritzmann laboratory.

Motor Activity Associated with Flight Turns

Over the last six months, work in the Willis Lab at CWRU has focused on comparing the guidance algorithms used by walking and flying insects to track odor plumes. These studies have included behavioral experiments, simulation and robotic experiments with CWRU's Quinn Lab, and the ongoing analysis of muscle activation patterns underlying free-flight maneuvering during odor-modulated navigation.

Collaboration between the Willis Lab and the Quinn Lab over the course of the research grant has resulted in significant progress in developing control algorithms to support chemical plume tracking behavior in autonomous walking and flying vehicles. This research, using both modeling and robotic approaches, has also led to reconsidering the existing hypotheses for how flying moths and walking cockroaches use olfactory and other sensory information to track airborne chemical plumes. One study performed by a CWRU M.S. student, developed an ultrasonic anemometer to detect wind speed and direction, and interface circuitry to interface wind and chemical detection systems with a wheeled koala® robot (Bailey et al., 2005). Ongoing robotic and simulation modeling work has included studies of control algorithms for plume tracking in 2D and 3D space (Edwards et al., 2005), the integration of multiple sensory inputs for odor tracking flight control (Rutowski et al., 2006a), and an algorithm that enables a flying agent to maintain its flight speed and altitude using only optic flow input (Rutkowski et al., 2006b).

Behavioral experiments performed in the Willis Lab have focused on the response of flying moths to plumes with different spatial distribution of odor (Morrison and Willis, in prep.), and comparing these responses to those of walking cockroaches to similar plumes (Willis and Avondet, 2005). A particular focus has been on the role of antennal postures and movements in plume tracking behavior. To date, results have shown that male moths tracking plumes in different wind speeds, and thus experiencing different amounts of aerodynamic drag on their antennae, maintain the same antennal posture regardless of the wind speed. These results, together with what is known about the sensori-motor control of airspeed in other insects, suggests that the moths are actively maintaining their antennae in a specific posture possibly to detect the moths airspeed. Associated work in the laboratory of a Dr. T. Daniel (Univ. Washington, Seattle), and funded by the Willis Lab ONR-MURI grant, suggests that the antennae of *Manduca sexta* may also serve as Coriolis force detectors feeding back to the control of yaw. This work is currently in review for publication in the journal Science. Similarly, male cockroaches tracking plumes of female pheromone maintain their antennae in a stereotyped posture. These results suggest that the movement of antennae during olfactory behaviors maybe a compromise between their function as wind sensing organs and odor-detecting organs. Experiments in this area are ongoing. Recent experiments on multi-sensory inputs supporting chemical plume tracking in walking male cockroaches has shown that individuals with no visual inputs can track plumes just as well as intact individuals. In these experiments, the performance of intact males were compared to those that had their large compound eyes, and simple occelli covered with black paint. Males with only their compound eyes painted performed as well as intact males. However, males that had their simple eyes painted walked more slowly, and the only individuals in the entire experimental design that were unable to track the plume to its source were those with their simple eyes painted.

Recent results from ongoing analysis of recordings of muscle activity patterns from freely flying moths during odor tracking flight have revealed an association between bi-laterally symmetrical muscle activation and lateral movement during turning maneuvers. It has been observed that the indirect elevators of the wings, that cause the upstroke of each wingbeat cycle, shift the timing of their activation each wing stroke in an asymmetric way during the zigzag turning that characterizes pheromone tracking in these moths. The central nervous system (CNS) advances and delays the activation of these muscles in a predictable way associated with rightward and leftward turns. The commonly accepted model of flight maneuvering in insects like the moth *M. sexta,* is that the indirect flight muscles are *not* involved in steering. CWRU results suggest that this is not the case. Ongoing analysis will increase our sample size and enable the comparisons across multiple behavioral and motor performances of the same individual.

Implementation of Biologically Inspired Control into Robotic Systems

Neural control of a robotic leg: One particularly interesting project that has begun in the past year is the implementation of a neurally-based control system for insect leg movement in a robot model. This model will serve as a means to test hypotheses regarding the neural control of leg movement, and it additionally holds promise for the reduction of control complexity in legged robots.

The control system was developed by Örjan Ekeberg at the Royal Institute of Sweden, with Marcus Blümel and Ansgar Büschges in Cologne, Germany based upon neurobiological experiments on stick insects. It is the most complete description of the local reflexes that have been documented for the stick insect, and has successfully moved the legs of a dynamic model insect. The control system consists of a bistable pattern generator for each joint, which changes states (e.g. from flexion to extension) based on sensory information from the leg. This sensory information is of course in turn influenced by the activation of the joints and the interaction of the leg with the environment. This control method, which we term Sensory Coupled Action Switching Modules (SCASM), is shown in Fig. 6 and described in (Lewinger et al. 2006, Ekeberg et al. 2004).

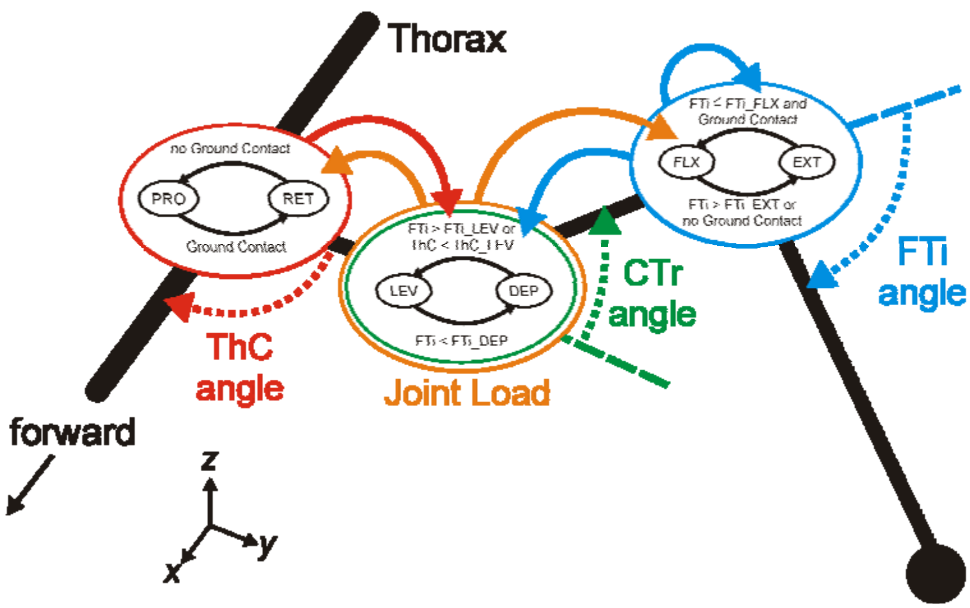

Figure 6. Graphical representation of the bi-stable pattern generators controlling each joint, showing the flow of sensory information between joints. The transition rules represent the controller used for three separate walking systems; only the thresholds differ between the models.

A collaboration was initiated with the Cologne group that proposes developing robotic stick insect and cockroach legs to be controlled by this model. Upon completion, the dedicated robotic models to test hypotheses such as our notion of how inside turning occurs can then be used. At this time the stick insect leg has been constructed (Fig. 7, left) and can make stepping movements under control of the stick insect model.

Two CWRU students have taken this leg and a two-leg robotic test platform (Fig 7, right) to Cologne to work with the Büschges laboratory in improving the leg controller, and collaborating on the development of a unified experimental interface for the various simulations and robotic models under development. It is believed that these dedicated robotic models will provide very powerful tools for testing neurobiological hypotheses.

For this project, previous lab experience with RTLinux has been leveraged to build software capable of implementing this type of control scheme, which represents biological motor systems for robot control with real-time parameter modification. Feed-forward torque control using small electrical servomotors for simulation of muscle function have also been implemented.

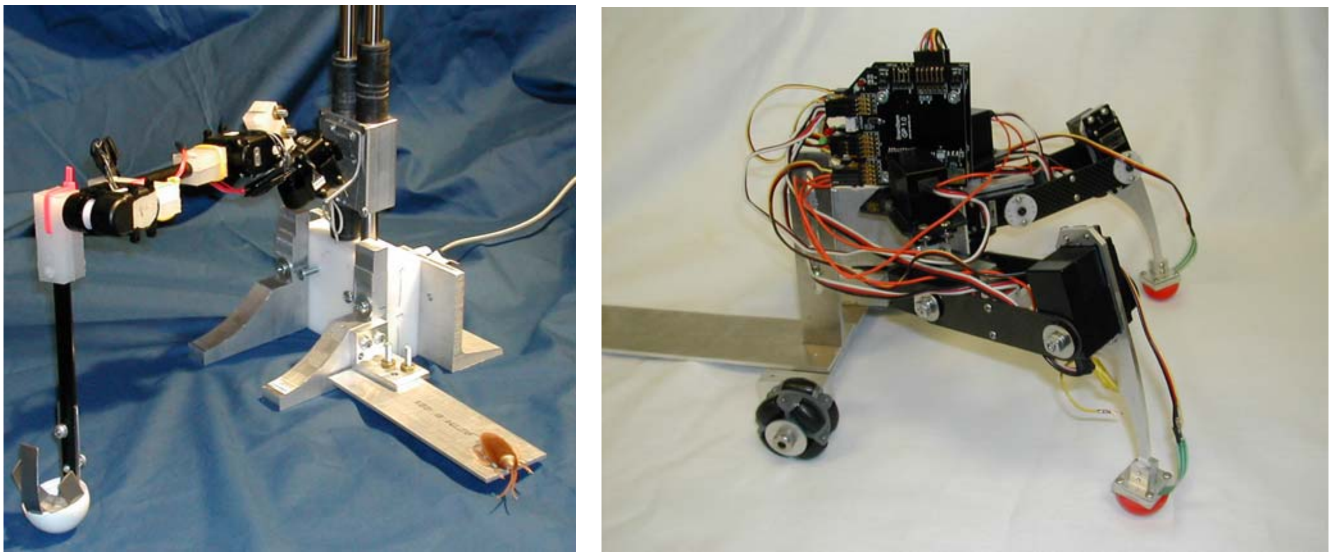

Fig. 7 LEFT: Single-leg scale model of a stick insect middle leg for biological experimentation. This view is from the front; the bar extending to the bottom right indicates the orientation of the thorax in the horizontal plane. RIGHT: Two-leg platform for implementation of SCASM in low-power mobile robots.

The same SCASM architecture has successfully produced walking motions which adapt to environmental changes in three systems: the original simulation, the single-leg robotic stick insect model and a two-leg robot test platform. In the animal this control architecture provides muscle commands; all three of the artificial systems have required simple muscle models to function successfully.

It has been shown that very simple muscle models will allow system operation (paper submitted to ICRA 2007) (See Fig. 8). Further research will investigate the extent to which increasing muscle model complexity would be useful from a robot control point of view.

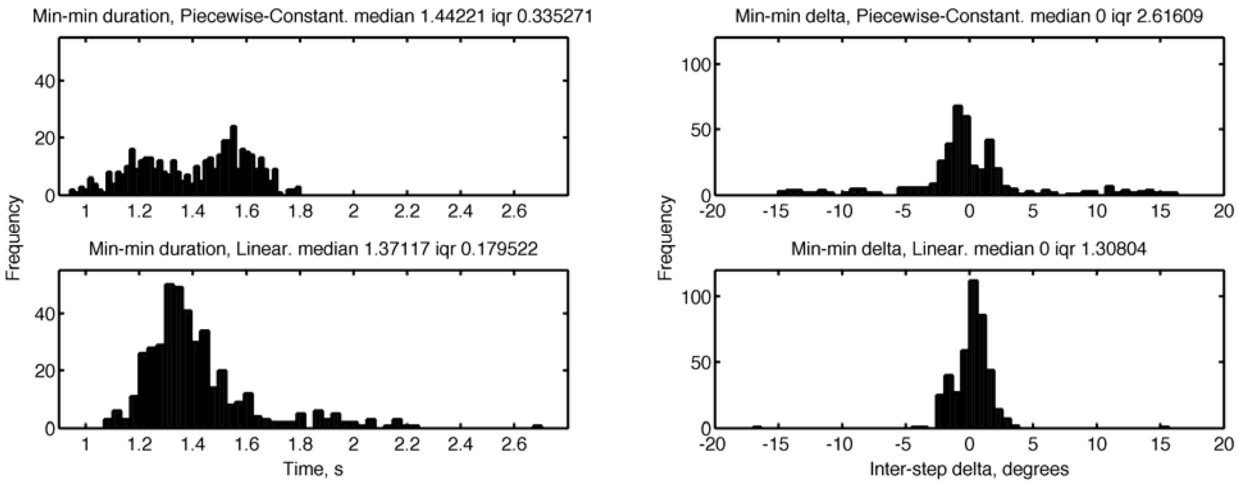

Fig. 8 A demonstration of the improvement in forward stepping when a simple linear muscle model is implemented at one joint (bottom graphs). LEFT: Histograms showing the distributions of durations of the entire step cycle, as measured from one minimum of ThC angle to the next (the point at which the foot is lifted and swing begins). The medians do not differ significantly according to the Wilcoxon test ($p=0.22$), and the distributions differ with $p = 1x10^{-8}$ according to the Kolmogorov-Smirinov test. Note the bimodal behavior in the system without the linear muscle model. RIGHT: The distributions of difference of the minimum ThC angle from step to step. The medians do not differ significantly according to the Wilcoxon test ($p=0.14$), but the distributions differ with $p = 3.7x10^{-5}$ according to the Kolmogorov-Smirinov test. The lack of the wide tails on data taken using the linear muscle model indicates a more consistent placement of the foot at transition from stance to swing.

Cockroach EMGs control robot leg: Several other robot control system projects at CWRU implement the use of cockroach EMGs to control a robot leg. A simple open-loop transformation from EMG to inlet valve commands for Braided Pneumatic Actuators (BPAs) has been developed and tested on walking behavior, driving artificial muscles at the CTr joint of a robot model (Fig. 9, left) with EMGs from corresponding muscles in the animal. It uses hardware-in-the-loop error minimization on an RT-Linux system to identify appropriate transformation parameters which make the EMG-driven robot motion most closely resemble the observed animal behavior (Rutter, Mu et al. 2006, and a paper submitted to ICRA 2007) (Fig. 10). This work suggests that this approach holds promise for use as a tool in the investigation of (insect) musculoskeletal systems. CWRU is currently conducting an initial investigation into what changes are necessary in this transformation to represent turning behavior, with the expectation that this could improve the understanding of changes between these behaviors in properties of the animal's neuromuscular transform. The simplicity of the transformation also suggests that in cases where EMGs are used as a system control input, the use of BPAs can reduce control system complexity.

For this project, research was completed on functional cockroach joint anatomy both for determining the joint geometry and range of motion for this model, and the degrees of freedom necessary for a robotic cockroach leg model based on the stick insect model above. Together with results from the EMG modeling work, these data have suggested further improvements, several of which will be implemented in what will be the most functionally accurate robotic model of a cockroach leg yet built (Fig. 9, right).

Fig. 9: LEFT: a close-up of the right middle leg of Robot V as modified for this work. CENTER: a LEGO kinematic model which uses the results of the functional anatomy studies. One copy of this model resides in the Ritzmann laboratory, the other in the Quinn laboratory. RIGHT: This functionally accurate robot model of a *Blaberus* middle right leg will make use of cabled artificial muscles for actuation, in order to allow joint ranges of motion observed in the animal.

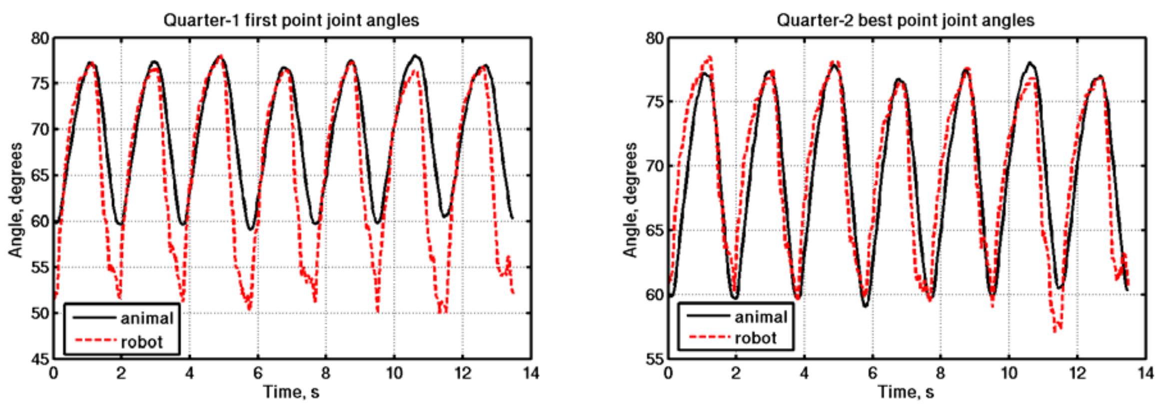

Fig. 10: EMG-driven joint angles before (left) and after (right) the error minimization used to find appropriate transformation parameters.

SUMMARY

CWRU has made significant progress in describing transitional behaviors in insect walking and in flight. Quantitative descriptions of the complex decisions that a cockroach makes in deciding to climb over or tunnel under a barrier has positioned researchers for examining discrete brain lesions in order to pin point where and how these decisions are made. Documentation of turning movements developed hypotheses regarding how descending cues might alter local reflexes to turn the animal while retaining stability. Lesions in the brain and subsequent recordings are beginning to demonstrate how the descending commands might be formulated within the brain. Finally, a robotic leg that was developed shows great promise as a hardware model of the control system, and could play a critical role in testing our hypotheses at a systems level.

The results that were obtained have positioned CWRU to move ahead with new funding initiatives. The brain recording and stimulation projects that were initiated under this recently completed effort, are now funded by an NSF grant to the CWRU Ritzmann Laboratory. Meanwhile, the projects that were undertaken to understand the alterations that occur at the local control level in response to descending commands is being pursued in a follow-on proposal to AFOSR. This proposal also includes development of the robotic leg hardware model. These two projects, which spun-off of the Eglin funded research, will continue to complement each other as CWRU continues to strive for an understanding of how insects control movement through complex terrain.

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APPENDIX A.

Research Output Generated During Period of Grant

Refereed Publications

1. Ritzmann, R.E., R.D. Quinn and M.S. Fischer (2004) Convergent Evolution and Locomotion through Complex Terrain by Insects, Vertebrates and Robots. *Arth. Struct. Dev.* **33(3)**:361-379.
2. Ritzmann, R.E., R.D. Quinn and M.S. Fischer (2004) Arthorpod locomotion systems: from biological materials and systems to robotics - Editorial. *Arth. Struct. Dev.* **33(3)**:183-185.
3. Rutkowski, A.J., Edwards, S., Willis, M.A., and R.D. Quinn (2004) A Robotic Platform for Testing Moth-Inspired Plume Tracking Strategies, IEEE International Conference on Robotics and Automation (ICRA'04), New Orleans.
4. Bailey, J.K., Willis, M.A, Quinn, R.D. (2005) A Multi-sensory Robot for Locating the Source of Wind-borne Chemicals. Conf. on Advanced Intelligent Mechatronics (AIM'05), Monterey, CA.
5. Edwards, S., Rutkowski, A.J., Quinn, R.D., Willis, M.A. Moth-Inspired Plume Tracking Strategies In Three-dimensions. *IEEE International Conference on Robotics and Automation* (ICRA'05), Barcelona. Lambrecht, B.G.A., Horchler, A.D., and Quinn, R.D., (2005) A Small Insect Inspired Robot that Runs and Jumps, 2005 IEEE International Conference on Robotics and Automation (ICRA '05), Barcelona, Spain.
6. Daltorio, K.A., Horchler, A.D., Gorb, S., Ritzmann, R.E., Quinn, R.D. (2005) A small wall walking robot with compliant adhesive feet, 2005 IEEE/RSJ International Conference on Intelligent Robots and Systems (IROS05), Edmonton, Canada.
7. Lewinger, W.A., Harley, C.M., Ritzmann, R.E., Branicky, M.S., Quinn, R.D., (2005) Insect-like Antennal Sensing for Climbing and Tunneling Behavior in a Biologically-inspired Mobile Robot. IEEE International Conference on Robotics and Automation (ICRA'05), Barcelona.
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12. Willis, M.A. and J.L. Avondet (2005) Odor-modulated orientation in walking male cockroaches, *Periplaneta americana* (L.), and the effects of odor plumes of different structure. *Journal of Experimental Biology* 208: 721-735.

13. Willis, M.A. (2005) Odor-modulated navigation in insects and artificial systems. *Chemical Senses* 30: i287.
14. Kingsley, D.A., Quinn, R.D., Ritzmann, R.E. (2006) A cockroach inspired robot with artificial muscles, IEEE IROS'06, Beijing.
15. Lewinger, W.A., Watson, M.S., Quinn, R.D. (2006) Obstacle Avoidance Behavior for a Mobile Robot Using Binaural Ultrasonic Sensors. IEEE IROS'06, Beijing.
16. Morrison, E.A. and Willis, M.A. Pheromone-mediated moth tracking behavior: *Manduca sexta* flight patterns along variously shaped plumes. Journal of Experimental Biology (in prep).
17. Ridgel, A.L., Alexander, B.E. and Ritzmann, R.E. (2006) Descending control of turning behavior in the cockroach, *Blaberus discoidalis. J. Comp. Physiol. A.* (in press).
18. Rutkowski, A.J., Willis, M.A., Quinn, R.D. (2006a) Simulated Odor Tracking in a Plane Normal to the Wind Direction. IEEE International Conference on Robotics and Automation (ICRA'06), Orlando.
19. Rutkowski, A.J., Willis, M.A., Quinn, R.D. (2006b) Biologically Inspired Self-motion Estimation using the Fusion of Airspeed and Optical Flow. American Control Conference, Minneapolis, MN.

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1. Kingsley, D.A., Quinn, R.D., Ritzmann, R.E., (2003) "A cockroach inspired robot with artificial muscles," Int. Symposium on Adaptive Motion of Animals and Machines (AMAM'03), Kyoto, Japan.
2. Mu, L. A.L. Ridgel, , B.E. Alexander, R.E. Ritzmann (2003) The role of brain neuropils during turning in the cockroach. *Soc. Neuroci. Abstr. CD ROM* **29**: Prog Numb. 606.4.
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11. Daltorio, K.A., Horchler, A.D., Gorb, S., Ritzmann, R.E**.,** Quinn, R.D. (2005) A small wall walking robot with compliant adhesive feet, Proceedings of Climbing and Walking Robots Conference (CLAWAR'05), London, U.K., September, 2005.

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18. Daltorio, K.A., Wei, T.E., Gorb, S.N., Ritzmann, R.E., Quinn, R.D. (2006) Insect-inspired foot geometry for rotating legs on a climbing robot. *Soc. Neuroci. Abstr. CD ROM* **32**: 449.14.

19. Harley, C.M. Predina, J.D., Ritzmann, R.E. (2006) Responses to incomplete sensory information in cockroach climbing behavior. *Soc. Neuroci. Abstr. CD ROM* **32**: 449.12.

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1. Lewinger, W.A., Harley, C.M., Ritzmann, R.E., Branicky, M.S., Quinn, R.D., (2005) Insect-like Antennal Sensing for Climbing and Tunneling Behavior in a Biologically-inspired Mobile Robot. IEEE International Conference on Robotics and Automation (ICRA’05) Video Proceedings, Barcelona, April 2005.- Best Video Award.

2. Daltorio, K.A., Gorb, S., Peressadko, A., Horchler, A.D., Ritzmann, R.E., Quinn, R.D. (2006) Wall-Climbing Mini-Whegs™. IEEE International Conference on Robotics and Automation (ICRA ‘06) Video Proceedings, Orlando.

3. Lewinger, W.A., Watson, M.S., Quinn, R.D. (2006) Obstacle Avoidance Behavior for a Mobile Robot using Binaural Ultrasonic Sensors. IEEE IROS’06 Video Proceedings, Beijing.

Invited Presentations:

1. Quinn (2003) “Biorobotics,” Great Minds, Great Friends (donor appreciation event), December 2003.

2. Ritzmann, R.E. and R.D. Quinn (2003) “Control of Legged Locomotion Over Complex Terrain By Cockroaches and Robots” IGERT Research Symposium at Carnegie Mellon University, Pittsburgh, PA June 27-29, 2003.

3. Ritzmann, R.E. (2003) “Control of Legged Locomotion Over Complex Terrain By Cockroaches and Robots” American Behavior Society symposium. “Mechanisms of Behavioral Switching”, Boise State University, Boise, Idaho, July 20, 2003.

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Press Coverage

1. Featured in Discovery Channel Television Show “UItimate Impact” shown in Canada and France, 2003.
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4. Featured in Animal Planet Show “Buggin’ with Ruud” to be aired in October, 2005.

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